

The University of Chicago

GERMINATION OF POPULU
GRANDIDENTATA AND P. TREMULOIDES
WITH PARTICULAR REFERENCE
TO OXYGEN CONSUMPTION

A DISSERTATION SUBMITTED TO THE
FACULTY OF THE DIVISION OF THE BIO-
LOGICAL SCIENCES IN CANDIDACY FOR
THE DEGREE OF DOCTOR OF PHILOSOPHY

DEPARTMENT OF BOTANY

1933

By

MILDRED ELIZABETH FAUST

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GERMINATION OF *POPULUS GRANDIDENTATA* AND
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CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 472

MILDRED E. FAUST

(WITH ONE FIGURE)

Introduction

Populus tremuloides Michx. and *P. grandidentata* Michx., which are known to reproduce chiefly by means of root shoots, produce seeds in great abundance in parts of the eastern and central United States. In these regions seedlings are not rare, although most of the reproduction, particularly following burns, is by means of root shoots. Where there is sufficient rainfall there are usually thousands of seedlings germinating on the old leaves or moist soil under or near the mature trees. Few if any of these ever reach more than a few inches in height.

P. tremuloides, which is one of the most widely distributed trees in the western hemisphere, as well as *P. tremula* L., a parallel species in the eastern hemisphere both as to habits and distribution, has short lived seeds which are found in abundance only in certain portions of its range. In Sweden, LAGERBERG (8) states that LOWENHJELM found difficulties in germinating the seeds since they remain viable for only three weeks. PEARSON (12), WEIGLE and FROTHINGHAM (13), and others find that seeds of *P. tremuloides* are not viable under normal conditions for more than three weeks. According to BAKER (2) and PEARSON (12), few seeds have been found in Utah. The latter has also found that in central Utah, owing to the short period of viability, it is difficult for seedlings to become established, except in locally wet places, as the surface of the soil is dry and rains are infrequent at the time of seed dispersal. This almost total absence of seedlings of *P. tremuloides* in such regions as Utah, as well as the small number which persist in other sections, raises the question as to the conditions under which germination and growth are possible.

An outstanding example which answers this question in part is

found at Strawberry Lake, Utah (altitude 7560 feet), where aspen is abundant in the adjacent hills. According to data obtained from W. P. Cottam, the reservoir was completed in 1912 and by June, 1913, 6000 acre-feet of water were impounded. In 1922 the water reached the spillway and again a year later. Since 1923 the water has never filled the lake, and today (1933) there are some 4900 acres exposed which were under water in 1923. The sagebrush which covered this shore region was killed through inundation and the barren opened to invasion. In 1928 the writer found intermingled with the dead sagebrush a great number of seedlings of *P. tremuloides*. Here the ground water of the denuded area was the important factor in establishing the aspen seedlings and supplied the deficiency ordinarily encountered in Utah where the climatic factors are the determiners.

From observation and repeated tests it is evident that seeds of both species of aspen will germinate under a varied range of environmental conditions as long as sufficient moisture is provided. Germination continues unhampered when the seeds are totally submerged in water.

Since moisture appears to be a critical factor in the establishment of these seedlings, and since the seedlings are relatively short lived, it was pertinent to study the effects upon viability of drying the seeds for varying lengths of time and thus of prolonging viability. Temperature studies on rate and percentage of germination were made on seeds of various ages and moisture contents, as well as tests of oxygen consumption at a constant temperature.

Seeds of *P. grandidentata*, which are produced in much greater abundance than those of *P. tremuloides* in the immediate vicinity of study, were used in most cases. It was found that there is practically no difference in the characteristics of the seeds of the two species. The catkin of the former is larger, being about 6 inches long and containing approximately 1000 viable seeds. It is produced a few days later than that of *P. tremuloides*, and before the leaves instead of with or after them.

The term "germination" as here used indicates a point at which the hypocotyl has grown out of the seed coat just far enough to raise one end of the seed from the substratum.

Material and methods

COLLECTING.—The seeds used for detailed studies were collected from trees growing in the crevices of the Onondaga limestone in the vicinity of Syracuse, New York. Records at Syracuse since 1922 show that anthesis for both species varies from March 19 to April 12. From 1927 to 1933 *P. tremuloides* seeds matured from May 10 to 20 and those of *P. grandidentata* from May 12 to 27.

The best time for collecting is on a clear calm day; however, seeds collected in the rain have retained 100% viability at 5° C. for at least one year. The seeds used for study were collected from catkins picked from the trees when the seeds were a light straw color. Those collected before reaching the characteristic straw color do not ripen completely and yield approximately 50% germination.

TRANSPORTATION.—The best method found for transporting seeds in the green catkins over long distances was packing them loosely in fine cheesecloth inserted in burlap bags. One lot of seeds was in transit for three days in extremely hot weather and maintained 100% viability after storage at 5° C. for two years.

DRYING.—Within an hour after collection, the catkins were spread out one or two layers thick in large shallow pans out of direct sunlight in an inside room of uniform temperature. In 1932 both an aneroid barometer and a Julien and Friez hygrothermograph were placed in this drying room. The mean atmospheric pressure for the first two weeks of drying (that is, from May 26 to June 8) was 29.92 inches. This varied from 29.60 to 30.25 inches. The mean temperature was 23.61° C. with a variation of from 20° to 26° C. The mean relative humidity of 8:00 A.M. and 12 noon was 48.50% with a range of from 27 to 66%.

The best length of duration of drying is from three to eight days. In 1930, when the largest number of seeds were collected, both species yielded 100% germination when first collected. Tests at 29° C. were made for seeds dried one, two, three, four, five, six, eight, nine, and ten days and then stored at 5° C. Germination percentages for seeds of both species are similar except that the drop in viability comes sooner in *P. tremuloides*. Those of *P. grandidentata* dried one day showed a sudden drop in germination to 47% before fifteen days and were dead in three months. Those dried both nine and ten days

were dead in thirty-six months and those dried both two and four days were dead in forty-five months. The ones dried six days showed 14% germination in forty-five months and those dried both three and five days had 44 % viable after forty-five months.

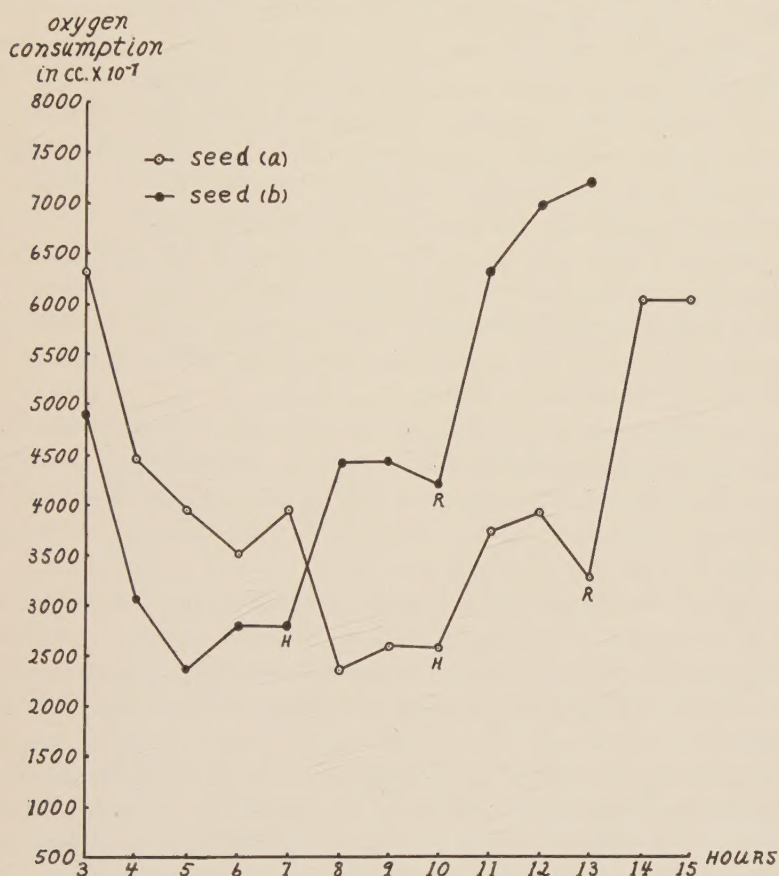


FIG. 1.—Hourly oxygen consumption of single seeds (a) and (b), *P. grandidentata* 1932, dried six days. Hypocotyl of seed (b) emerged two hours before that of seed (a), showing individual differences in germination. H, hypocotyl; R, root hairs.

CLEANING AND GRADING.—When the seeds had dried the desired length of time, the catkins were placed over a wire screen on top of an open box and were separated from the cotton by means of a heavy brush. The seeds which dropped through the screen were blown free

from chaff and graded through screens of 30 and 40 mesh to the inch. Seeds graded with the former screen were used for all the tests except as indicated later.

There is a definite parallel between the curves of germination of small and large seeds. The total percentage of germination of *P. grandidentata* 1928, which was dried four days and planted when thirteen to seventeen days old, showed an average germination of 45% for small seeds as compared with 96% for the large ones.

PLANTING.—All tests of seed germination, unless otherwise noted, were made in petri dishes containing two layers of thoroughly moistened filter paper with the excess water drained off.

The seeds will germinate whenever there is sufficient moisture. At the same temperatures the total percentages of germination are the same regardless of whether or not the seeds are totally submerged in water, or are on filter papers with varying amounts of moisture in similar or different sized dishes.

The percentage of germination was found to be comparable on filter paper (moistened with distilled water), sand of pH 7.0, and humus (in which the aspens grow) of pH 8.5. However, only 82% germinated on sand of pH 4.5 as compared with 98% on the other media.

Twenty-five to one thousand seeds were used for each germination test. In the studies of the effect of temperature upon germination fifty and one hundred seeds were used. It was found that fifty and usually twenty-five gave reliable results when the seeds were of high viability.

STORING.—The seeds were stored in three ways: (1) in open dishes in the laboratory, (2) in corked bottles in the laboratory, and (3) after 1930 in corked bottles at 5° C. in a General Electric refrigerator constant to $\pm 0.5^\circ$ to 1° C. The seeds occupied from one-half to one-fourth the volume of the bottles, which were opened for ventilation at various intervals.

After eighteen weeks of storage both in open dishes and corked bottles in the laboratory, seeds of both species gave germination percentages of 1. However, *P. grandidentata* 1930 which had been dried both three and five days before storage in a bottle showed 1% after twenty-two weeks. The latter remained 100% viable for twelve

weeks when dried five days, for eleven weeks when dried four days, for nine weeks when dried three days, and for seven weeks when dried nine days. *P. tremuloides* 1930 dried both two and four days before storage in bottles remained 100% viable for thirteen weeks. Any seeds stored in the open retained their 100% viability for only five weeks.

After storage in bottles at 5° C., seeds dried more than two days showed the greatest viability for long periods of time. Those of *P. grandidentata* 1930 which were dried for one day only and placed in a bottle in the laboratory had 76% germination at the end of one week and 0% in two weeks, while the same lot of seeds stored at 5° C. lost viability in twelve weeks.

Until 1930 an icebox of varying temperature was used for low temperature storage. Seeds kept in it fell off more rapidly in percentage of germination than did those kept constantly at 5° C. *P. grandidentata* 1929 and 1930, germinated at 29° C. when thirty-two weeks old, showed 29% for those of 1929 and 98% for those of 1930. After one year *P. grandidentata* 1929, dried five days, gave 1% germination; while that of 1930, also dried five days, gave 91% and was 76% viable after three years.

Cold storage (about 5° C.) of fully matured and dried seed has been found to be important for extensive prolongation of vitality of short lived seeds. NAKAJIMA (10) in his study of *Salix* found that storage under several conditions at a low temperature prolonged vitality. In one instance he obtained 53% germination after three hundred and sixty days. JOSEPH (6) finds that the vitality of parsnip seeds is prolonged decidedly by air drying to a certain low moisture content and subsequent storage in an icebox with frequent ventilation.

Germination results

TEMPERATURE RELATIONS

Germination of both species is not dependent upon light, and with sufficient moisture will take place at any temperature between 0° and 35° C. The General Electric refrigerator was used for germination at temperatures of 5° C. and below and ovens constant to $\pm 0.5^\circ$ C. for temperatures of 26°, 29°, 32°, 35°, and 38° C.

Seeds dried and stored under similar conditions, even though collected from different trees and in different years, gave similar germination percentages. Seeds of *P. tremuloides* 1930 and 1932 dried three days, before storing at 5° C. for one year, showed germination of 97% at 29° C. Seeds of *P. grandidentata*, stored and germinated under similar conditions, showed 100% in 1930 and 97% in 1932.

MAXIMUM, MINIMUM, AND OPTIMUM TEMPERATURES.—No particular attempt was made to determine the maximum, minimum, and optimum temperatures for the two species. After exposure for two weeks to the highest temperature used (38° C.), no seeds germinated. When these were transferred to both room temperature and 29° C., however, a number of them were found viable.

Seeds of *P. grandidentata* 1929, dried five days before storage on ice for twenty to twenty-three weeks, gave no germination at 35° C. but gave 39% at 32° C. and 20% at 29° C. A larger number of young seeds will germinate more quickly at 35° C., but complete (100%) germination is attained sooner at 29° and 32° C. Seeds up to one year old which have been frozen for several days and thawed at 5° C., as well as those kept constantly at 5° C., germinate in five days at 5° C.

The largest percentage of germination was attained at both 29° and 32° C. However, the sturdiest appearing seedlings were those from seeds germinated at temperatures from 5° to 29° C. Seedlings of *P. grandidentata* 1929 three weeks old were twice as tall when germinated at 29° as those germinated at 35° C.

Both species of 1930 seeds which were dried for periods of two, three, four, five, and six days and studied for a period of the first five weeks after collection showed curves for the rate and percentage of germination which were practically parallel at the three temperatures, 26°, 29°, and 32° C. The rate was always slower for those germinated at 26° and the average final percentage of germination was 98 as compared with 100 for those germinated at 29° and 32° C.

INITIAL GERMINATION.—Seeds of both species collected from the same trees over a period of six years have been found to show the initial germination in five hours at 29° and five days at 5° C. Occasionally the seeds of *P. tremuloides* germinate in four hours at 29° C. It is found that when seeds are germinated at a higher temperature (29° C.) the initial time becomes greater as the seeds age. For seeds of *P. tremuloides* 1930 dried three, four, and five days and

P. grandidentata 1930 dried four, five, six, nine, and ten days, initial germination at 29° C. occurs in five hours for a period of thirty-two weeks, then it increases to seven hours at forty-nine weeks, to nine hours at one year, and from twelve to twenty-four hours at three years.

P. tremuloides seeds of the same lot as the preceding but dried two days required for initial germination only seven hours at the end of one year; while *P. grandidentata* seeds from the same lot but dried three days required seven hours at forty-nine weeks, eight hours at one year, and from twelve to eighteen hours at three years. The latter retained 100% viability for one year and dropped to 84% in three years.

MICROCHEMISTRY

Microchemical tests were made on two sets of one year old seeds of *P. grandidentata* 1930 with 0% and 92% germination, on one set of *P. tremuloides* 1930 with 90%, on three week old 1931 *P. grandidentata* and *P. tremuloides* with 100%, and on *P. grandidentata* 1931, three day old seedlings.

The contents of the seeds of both species at the same age are comparable. The outer layer of the seed coat of the resting seeds is composed of cellulose and the inner of unknown (yellowish brown) material. The outer wall becomes partially broken down into sugars (mostly sucrose) and starch in the year old viable seeds and decidedly so in the dead ones. In the latter the inner wall breaks down, to a lesser extent, into sugars (some glucose) and starch.

The storage products in the two (or three) cotyledons are fats and proteins, these being in similar amounts and arrangements in the viable young and year old seeds but reduced in amount in the dead seeds.

In the seedlings the fats are scattered throughout the cotyledons but concentrated near the veins. The proteins are near the veins and at the base of the hypocotyl. Small amounts of glucose, fructose, and sucrose are scattered throughout the seedling.

The storage compounds appear to have some bearing upon germination and after-ripening. JONES (5) found that in the genus *Acer* the short lived seeds (*A. saccharinum*) have storage compounds composed mainly of sugars, while the comparatively long lived ones which require after-ripening (*A. saccharum*) have compounds of pro-

teins and fats. Here aspen seeds, with storage compounds of fats and proteins, are found to be short lived, at least in temperate climates. Upon submission to low temperatures, however, they become comparatively long lived.

MOISTURE CONTENT

Moisture determinations of seeds of *P. grandidentata* 1932 were made from averages of two lots of seeds of 1 gm. each which were ground fine in an agate mortar. They were then dried in a vacuum desiccator over concentrated sulphuric acid and kept in a constant temperature oven at 60° C. The moisture percentages after the seeds had been in storage twelve weeks in closed bottles at 5° C. are shown in table II.

When the seeds are heated above 60° C. there is decided discoloration, but from a few tests, sufficient only to give a suggestion, it appears that a higher temperature does not appreciably alter the percentage of moisture of those air dried between four and eight days. Although the seeds of the two species vary slightly in size, the moisture percentage is similar in both when submitted to the same drying conditions. Seeds of *P. tremuloides* 1930, which were dried at 104° C., seven months after collection showed 8.62% moisture. These had been dried for five days before storage at 5° C.

Both 1931 species were dried in a vacuum oven at 79° C. Those of *P. tremuloides*, which were dried five days before storage and the moisture determinations made after they were twenty-six days old, showed 8.83%. Those dried four days before storage and tested after nineteen days, showed 8.85% moisture. *P. grandidentata*, dried for six days before storage and tested when fifteen days old, showed 8.45% moisture. The 1931 seeds of *P. tremuloides* were 100% viable and those of *P. grandidentata* were only 50% viable.

Other writers have also found that longevity of seeds is increased by reduction in the moisture content. JOSEPH (6) found that for parsnip seeds, somewhere below 6.13% moisture at room temperatures appeared to be the "critical moisture content."

Oxygen consumption

A Thunberg microrespirometer, modified by FENN (1927) and later by OBRESHKOVE (OBRESHKOVE and BANTA 11), was used for the study of the oxygen consumption of both seeds and seedlings.

The extreme sensitiveness of the apparatus is apparent by its capacity for measuring accurately and directly the oxygen consumption of ten resting seeds or a single germinating seed of *P. grandidentata*, the average weight of each being 0.0000941 gm.

Attempts were made to use KRAJNÍK'S (7) microrespirometer, an apparatus first used on plants (strawberry fruits) in this country by GERHART (3). Owing to its large size, however, and the fact that it could not be entirely submerged in the water bath, it lacked the sensitivity necessary for reactions of very small objects.

The microrespirometer, which is composed of two glass bottles connected by a capillary containing a kerosene drop, was totally sub-

TABLE I
OXYGEN CONSUMPTION FOR SEEDS OF *P. GRANDIDENTATA* 1932

MICRORESPIROMETER TEST	OXYGEN CONSUMPTION PER SEED PER MINUTE IN CC. $\times 10^{-7}$				
	SEED 0	SEED 2	SEED 4	SEED 6	SEED 8
First hour.....	53.499	25.309	10.823	14.640	9.656
Second hour.....	52.642	19.701	14.485	14.484	14.374
Third hour.....	49.371	23.985	17.910	21.804	16.197
Fourth hour.....	48.437	25.153	20.091	20.168	19.076
Average.....	50.987	23.537	15.827	17.774	14.826

merged in a Freas waterbath with a thermostat control set at 25° C. and sensitive to $\pm 0.005^\circ$ C. It was absolutely necessary to keep the temperature as nearly constant as possible. A variation of more than $\pm 0.01^\circ$ C. caused enough fluctuation in the volume of oxygen consumed to render the results worthless. In order that the microrespirometer attain the exact temperature of the waterbath, it, with its contents of a 2% solution of NaOH and the seed or seeds, was submerged in the bath for an hour before it was closed to the air and then left another hour before readings were taken.

For resting seeds readings were taken hourly over a period of four hours (table I). The oxygen consumption is represented in cubic centimeters times 10^{-7} per seed per minute. Seed 0 is the lot of seeds not dried at all, seed 2, that dried two days, etc. The recorded tests are from those lots of seeds which showed 100% germination after removal from the microrespirometer. Care was taken at all times to

handle the seeds as little as possible when removing from storage and placing in the microrespirometer.

The seeds used were those of *P. grandidentata* 1932 which had been dried zero, two, four, six, and eight days. Ten seeds were used and an average of five tests is recorded for each hour. Repeated tests at the immediate close of the drying period and also within two months after they were stored showed comparable amounts of oxygen consumption.

As the moisture content of the seeds decreases the oxygen consumption decreases (tables I and II). Such a correlation has been found for certain other seeds by a number of workers, notably BAILEY (1), JAQUOT and MAYER (4), and MAIGE and NICOLAS (9).

TABLE II
OXYGEN CONSUMPTION AND MOISTURE ABSORPTION FOR SEEDS OF *P.*
GRANDIDENTATA 1932 DRIED FOR DIFFERENT LENGTHS OF TIME

NO. OF DAYS DRIED	AVERAGE 4 HOURS OXYGEN CONSUMPTION	PERCENTAGE MOISTURE ABSORBED	MOISTURE CONTENT	PERCENTAGE GERMINATION AT TESTS	PERCENTAGE GERMINATION AT END OF ONE YEAR
0	50.987		49.22	100	0
2	23.537		30.52	100	0
4	15.827	11.30	9.18	100	67 (poor)
6	17.774	12.07	6.65	100	95 (healthy)
8	14.826	10.02	7.52	100	95 (poor)
73			6.97	100	

As noted in table I, there is a gradual increase in the amount of oxygen consumed during the first four hours of the tests of seeds 4, 6, and 8. It was found that these absorbed an appreciable amount of water from the NaOH solution (table II).

The comparatively large amount of oxygen consumed in freshly harvested seeds drops to approximately half after one day of drying. After the third day of drying there is no considerable difference in the amount consumed. Of the 1932 seeds those dried six days are the best from the standpoint of longevity, for after thirty-two months 85% of them were viable as compared with 65% of seed 8 and 17% of seed 4.

The most striking results were obtained when the oxygen consumption of a single seed placed on moist filter paper in the micro-

respirometer was checked at five-minute intervals. The seedlings were all taken from seed 6 which had been in storage at 5° C. for two months.

In order to obtain a relative idea of the oxygen consumed during the first two hours, a seed (*c*) was placed in the microrespirometer for only fifteen minutes before readings were taken. Using round numbers for cubic centimeters of oxygen times 10^{-7} , during the second fifteen minutes it absorbed 13,300; during the third fifteen minutes, 4200; and the fourth fifteen minutes, 1700. Two other seeds (*a*) and (*b*) were left in the microrespirometer for one hour before it was closed and the readings taken for the second hour of germination. Seed (*a*) consumed approximately 47,200 and (*b*) 41,100 cc. times 10^{-7} . Figure 1 illustrates the results of the latter two seeds from the third to the fifteenth hours of germination and the third to the thirteenth hours respectively. Here the results are noted after the seeds and apparatus had been in the bath for two hours, as was done with the resting seeds. These two seeds were chosen because they illustrate individual differences in initial time of germination. The hypocotyl of seed (*b*) was 1 mm. long and the crown of root hairs 0.5 mm. long (one-half final length) at the end of thirteen hours, while it required fifteen hours for those of seed (*a*) to attain the same lengths.

Summary

1. *Populus tremuloides* and *P. grandidentata* produce seeds in great abundance in central and eastern United States. The former seeds mature approximately three days earlier than the latter. From six to ten weeks elapse between anthesis and maturation of the seeds.

2. Seeds collected when a light straw color and dried at once retain their viability the longest.

3. The best length of time for drying is from three to eight days in a room of uniform temperature of about 24° to 25°C. Seeds dried only one day lose viability in thirteen weeks, even when placed at 5° C.

4. Small seeds do not germinate so readily nor retain their viability so long as large ones. This applies to individuals within the species.

5. Seeds showed the highest percentage of germination in media of pH 7.0 to 8.5.

6. Except when the viability is low, fifty seeds are sufficient for showing accurate percentages of germination.

7. A constant low temperature (approximately 5° C.) was found best for prolonging viability.

8. Seeds have been found to retain 100% viability for as long as thirteen weeks when placed in corked bottles in the laboratory and for five weeks in open dishes. Most of these lose their viability after eighteen weeks but occasionally show 1% at twenty-two weeks.

9. Seeds germinate whenever there is sufficient moisture (even when submerged) between temperatures of 0° and 35° C. Freezing for several weeks does not appear to injure the seeds when they are thawed at 5° C.

10. The largest percentage of germination is obtained at 29° and 32° C.; 35° to 38° C. appears to be too high but may only retard germination. The sturdiest seedlings are from seeds germinated at temperatures from 5° to 29° C.

11. The time for initial germination is usually five hours for seeds germinated at 29° and 32° C. This increases as the seeds age. Short initial germination time is correlated with high viability.

12. The seeds of both species are fatty and contain some proteins.

13. Seeds lose moisture rapidly during the first two days of drying. After three days there is little loss.

14. Oxygen consumption was studied by means of a microrespirometer of the closed system so sensitive that a temperature constant to $\pm 0.005^\circ$ C. was necessary for accurate results.

15. The extreme sensitiveness of the apparatus makes it possible not only to measure the oxygen consumption of ten resting seeds at half-hour intervals, but also that of a single germinating seed at five-minute intervals.

16. Oxygen consumption is high when the seeds are viable and contain much water. This decreases with the decrease in water content of the seeds.

17. The very great amount of oxygen consumed when the germinating seed first absorbs water drops to a minimum two hours before the hypocotyl emerges from the seed coat. It then rises rather abruptly for an hour, drops slightly in the next two hours, after which the crown of root hairs emerges. There is again a rather abrupt rise for an hour and then it becomes comparatively uniform.

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